Reference: *Biol. Bull.* **176:** 41–49. (February, 1989)

Suspension Feeding in Oscillating Flow: The Effect of Colony Morphology and Flow Regime on Plankton Capture by the Hydroid *Obelia longissima*

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Abstract. The effect of flow regime on the ability of the hydroid *Obelia longissima* to capture plankton was examined in a laboratory flume and a wave tank. Feeding effectiveness—the proportion of the gastrozooids with tentacles successfully capturing food in a fixed amount of time—is significantly greater in oscillating flow than in unidirectional flow at the same average velocity and particle flux. Thus quantitative feeding studies in unidirectional flow may seriously underestimate feeding in the field if flow in the natural habitat is unsteady. Increasing colony bushiness (weight/colony length) decreases feeding effectiveness in uni-directional and low frequency oscillating flow, but not in high frequency oscillating flow. Longer colonies (0.083 m) show significantly lower feeding effectiveness than short (0.033 m) colonies. This decrease in feeding effectiveness with increasing colony length and bushiness is offset by a rapid increase in polyp number with increasing colony length.

Introduction

Suspension-feeding organisms include representatives of almost every phylum, and the extreme radiation of many groups (*e.g.*, bivalve molluscs) has often been attributed to the acquisition of this habit (Jørgensen, 1966). Indeed, in benthic marine habitats, suspension-feeders are among the most conspicuous organisms. Because of the extreme prevalence of this lifestyle and the fact that many suspension feeders such as copepods form crucial links in the food web, suspension feeding mechanisms have attracted the attention of numerous biologists (*e.g.*, see reviews by Jørgensen, 1966, 1975, 1983).

Early studies of suspension feeding primarily examined particle capture by "active suspension feeders" (organisms that generate their own feeding currents) in still water (Jørgensen, 1966, 1975, 1983). More recently, with the use of unidirectional recirculating flumes to provide a well-characterized ambient current, it became possible to study suspension feeding in the laboratory by organisms that do not generate their own feeding currents, so-called "passive" suspension feeders (*e.g.*, Leversee, 1976; Taghon *et al.*, 1980; LaBarbera, 1981; Okamura, 1984; Patterson, 1984). Do these laboratory flumes provide sufficiently "realistic" flow regimes to permit extrapolation of the results of laboratory feeding studies to the performance of organisms in the field? Clearly, the answer to this question depends on the natural habitat of the organism under investigation.

The dynamics of flow in shallow water are often dominated by wave action. Although flow beneath waves is typically orbital, the orbits are compressed and flow is predominantly bi-directional (oscillating) close to the substratum (Bascom, 1964). Thus many shallow water, benthic organisms live in an oscillating flow habitat. If food capture by sessile organisms is neither quantitatively nor qualitatively different in oscillating flow regimes than in unidirectional flow regimes, then unidirectional flumes would provide an adequate system in which to study suspension feeding by most sessile organisms. If this is not the case, however, it will be necessary to re-evaluate studies of suspension feeding with greater attention to the dynamics of the flow regime in which the organism lives.

Suspension feeding organisms range from being rather rigid organisms (*e.g.*, mussels and scleractinian corals that maintain a constant morphology regardless of flow regime) to being flexible organisms (*e.g.*, hydroids that are deformed by moving water and are reoriented when

Received 22 July 1988; accepted 15 November 1988.

the flow direction changes). Flexibility must be important to a suspension feeder since deformation will affect flow (and consequently particle flux) around the organism (*e.g.*, if branches collapse together, flow slows through the colony). While there are a few studies of suspension feeding in flexible organisms (*e.g.*, Leversee, 1976; Okamura, 1984), these were made in uni-directional flow regimes, essentially steady-state situations. Holland *et al.* (1987) examine particle capture by the crinoid *Oligometra serripinna* in unsteady flow. The flow regime they used, however, provided brief periods (2 s) of reversed flow alternating with long (10 s) periods of flow in one direction. While this approximates some surge conditions, it is not a good approximation of fluid movement under waves. The purpose of this study is to measure particle capture by the hydroid *Obelia longissima*, a "representative" flexible organism, in uni-directional and oscillating flow regimes. This will permit evaluation of the importance of flow regime (unidirectional *vs.* oscillating) to suspension feeding organisms. I will also examine how flexibility may affect the performance of a suspension feeder.

Materials and Methods

Animal collection

Specimens of the thecate hydroid *Obelia longissima* were collected from the dock at Friday Harbor Laboratories, Friday Harbor, Washington. Colony selection from the field was randomized using a random number table. The animals were transferred to seawater tables where they were held no longer than 4 hours prior to their use in experiments.

Experimental design

A 3 by 2 factorial design was used to assess the effects of colony length and oscillation frequency on feeding by hydroid colonies. Feeding indices (defined below) were determined for colonies of 2 different lengths in each of 3 different flow regimes. The average length of short colonies was 0.033 m (S.D. = 0.005), while the average length of long colonies was 0.083 m (S.D. = 0.012). Flow regimes were: (1) uni-directional flow, (2) "low-frequency" oscillating flow at a frequency of 0.33 Hz with a peak velocity of 0.087 m/s, and (3) "high-frequency" oscillating flow at a frequency of 1.04 Hz with a peak velocity of 0.068 m/s. In all three flow regimes, the average (root mean square for oscillating flow) velocity was 0.025 m/s, comparable to that seen by these *Obelia longissima* in the field (Hunter, 1988). The high-frequency oscillation corresponds to wind-generated chop commonly experienced by *Obelia* in the field, while the low frequency oscillation was more like the waves generated by large boat (ferry) wakes (Hunter, 1988). Since the mean velocity and particle concentration was equivalent in all treatments, the mean number of particles moving past the colony per cross-sectional area of tank per unit time (particle flux) was also equivalent in all treatments.

Oscillating flow tank

Oscillating flow was produced using a wave tank (Hunter, 1988). The tank produced a uniform (less than 5% variation in velocity across the working section), smooth flow field. Oscillation frequency could be varied from a period of 4.0 s to 0.9 s at peak velocities ranging from 0.01 m/s to 0.25 m/s.

Unidirectional flow tank

Uni-directional flow was produced in a recirculating flow tank (Vogel and LaBarbera, 1978). The velocity profile across the tank was adjusted with baffles and the flow velocity did not vary by more than 7% of the mean velocity across the working section of the tank.

Food

Fresh plankton was used as the food source. Plankton was collected by towing a plankton net (80 μm mesh) alongside the pier at Friday Harbor Laboratories. The plankton was washed out of the net with seawater and then stained for 10 min with rhodamine B (0.005% in seawater). The stain solution was washed out of the plankton, using a 50 μm Nitex mesh to retain the plankton. The bulk of the remaining plankton ranged in size from 50 μm to 200 μm. It consisted of eggs, veligers, plutei, copepods, many larval crustaceans, and other types of invertebrate larvae.

The concentration of the stained "stock suspension" of living plankton was determined by counting a subsample (25 ml) in a Bugarov tray on a dissecting microscope. This permitted determination of the appropriate dilution for use in an experiment. The plankton concentration in the flow and wave tanks was adjusted to approximately 0.75 particles/ml immediately prior to each experiment.

The concentration of the same size range of plankton in the hydroid's habitat (adjacent to the pier) typically ranged from 0.05 to 0.9 (mean = 0.6, S.D. = 0.5, n = 10) particles/ml over the duration of this study, although there was a one-week period where the concentration of megalops larvae alone reached 1.05/ml. Thus the particle concentrations used in these experiments were comparable to those in the field, being slightly higher than mean field values. The experiments had to be kept short to prevent particle digestion before counting and thus it was necessary to use a slightly high particle concentration to assure a countable number of fed polyps in the small colonies.

The same stock suspension of plankton was used for each set of treatments on a given day. Thus, although the plankton composition changed through the season, the change was comparable across all treatments. The order of treatments was randomized each day to eliminate possible biases due to diel cycles of feeding activity. The treatment water was sampled immediately prior to and subsequent to the running of a feeding experiment. The particle concentrations in these samples were determined by counting as indicated above.

Measure of feeding effectiveness

To measure feeding effectiveness, every tentacle-bearing polyp in a colony was counted. Those polyps that took plankton were easily identified by the bright red color of the stained plankton contained within the coelenteron (gut). It was not possible to count individual plankton particles within a polyp, so it was assumed that all fed polyps consumed equivalent volumes of food. This was justified since, if the polyp fed at all, it was usually completely full (pers. obsv.). Typically, the fed polyp was bloated, completely filling the theca (the cup-like exoskeleton surrounding the polyp).

A feeding treatment lasted 15 min. Colonies fed for a longer time (up to 1 h) contained more fed polyps, indicating that the colonies were not satiated at the end of a 15-min feeding treatment.

Since larger colonies have more polyps, it was necessary to normalize the counts of fed polyps to compensate for simple size effects. Two normalizations were determined: (1) "polyp feeding effectiveness," a measure of how many polyps fed successfully, was defined as the fraction of polyps capable of feeding (gastrozooids fully differentiated and possessing intact tentacles) that actually captured food. (2) "Colony feeding effectiveness," a measure of feeding rate relative to the biomass supported by that food, was defined as the number of polyps that captured food divided by the mass of the colony.

Polyps were counted immediately after the experiment, so there was not enough time for digestion to alter the apparent number of fed polyps. As digestion proceeded (longer than 40 min), the stain moved down through the polyp into the common coelenteron (gut) of the colony. If the stain appeared below the level of the theca, the colony was not used.

Polyp feeding effectiveness is a ratio bounded between zero and one. All measures of polyp feeding effectiveness were arcsin transformed prior to statistical analysis (Sokal and Rohlf, 1969). Colony feeding effectiveness, however, may be greater than one, and was not transformed prior to analysis.

Effect of uni-directional flow velocity

Differences observed in feeding performance between uni-directional and oscillating flow might have been due to the fact that oscillating flows had higher peak velocities than did the uni-directional flows. To ascertain if increased flow velocity *per se* could produce higher feeding rates, feeding was measured at three velocities in uni-directional flow: 0.025 m/s, 0.050 m/s, and 0.10 m/s. The fast velocity (0.10 m/s) was greater than the peak flow velocity in any of the oscillating flow treatments. At a fixed particle concentration, however, faster flows provided a greater particle flux past the colony. To separate the effects of differing flux from those due simply to fluid velocity, two experiments were done. In the first experiment, the particle concentration was equivalent at each flow velocity. In the second experiment, particle concentration was adjusted to provide an equivalent particle flux at all three velocities.

Results

Oscillation frequency

Obelia colonies feeding in oscillating flow had a significantly higher polyp feeding effectiveness (# fed polyps/# polyps capable of feeding) than those colonies feeding in unidirectional flow at the same average particle flux (2-way ANOVA, $F_{(2,120)} = 22.7$, $P < 0.0001$, for flow effects) for both long and short colonies (Fig. 1). There was no significant difference in particle capture between colonies in the low-frequency and colonies in the high-frequency flow regimes (Student-Newman-Keuls post-hoc test, Damon and Harvey, 1987). This was true for both long and short colonies (2-way ANOVA, $F_{(2,120)} = 0.57$, $P = 0.57$, for interaction).

Similarly, colony feeding effectiveness (# polyps fed/colony dry weight) is greater in oscillating than in unidirectional flow (2-way ANOVA, $F_{(2,114)} = 5.58$, $P = 0.005$ for flow effects). Colony feeding effectiveness appeared directly proportional to oscillation frequency in long colonies. Short colonies had a higher colony feeding effectiveness in low-frequency oscillating flow than in unidirectional or high-frequency oscillating flow (Fig. 2). The interaction between flow regime and colony length was high, but not significant (2-way ANOVA, $F_{(2,114)} = 2.62$, $P = 0.08$ for interaction), suggesting that the difference in frequency dependence between long and short colonies was not significant.

Particle concentration

There were no significant differences in initial particle concentration (2-way ANOVA $F_{(3,120)} = 0.69$, $P = 0.56$) or particle depletion (2-way ANOVA $F_{(3,120)} = 0.91$, $P = 0.44$) during the experiment between any of the treat-

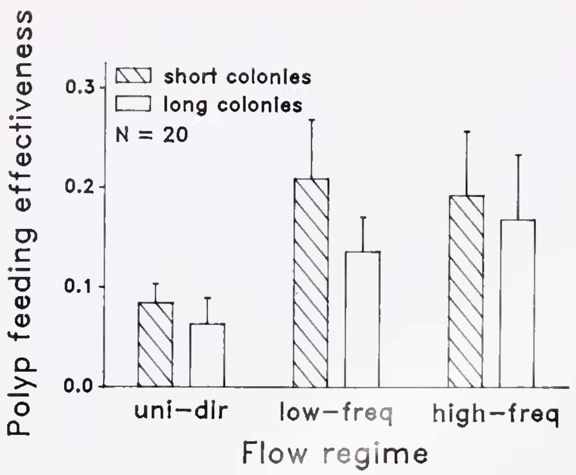

Figure 1. Polyp feeding effectiveness (number of fed polyps/number of polyps capable of feeding) in uni-directional flow, low frequency (0.33 Hz) oscillating flow, and high frequency (1.04 Hz) oscillating flow for long (0.083 m) and short (0.033 m) colonies. Error bars are 95% confidence intervals.

ments, indicating that the feeding effects were not due to differences in particle concentration between the treatments.

Colony length

Long colonies had significantly more fed polyps than short colonies (2-way ANOVA, $F_{(1,120)} = 34.7$, $P < 0.001$, for length). This simply reflects the fact that long colonies have more feeding polyps than short colonies. However, polyp feeding effectiveness (# fed polyps/# polyps capable of feeding) is actually less for long colonies than for short colonies (2-way ANOVA $F_{(1,120)} = 7.8$, $P = 0.006$ for length) (Fig. 1). In contrast, colony feeding effectiveness (# fed polyps/colony weight) is not significantly different for long and short colonies (2-way ANOVA, $F_{(1,114)} = 2.27$, $P = 0.14$ for length) (Fig. 2). This suggests that the increase in polyp number in larger colonies offsets the lowered polyp feeding effectiveness.

Colony bushiness

Bushiness was defined as the weight per unit length of colony. Polyp feeding effectiveness showed a slight decrease with increasing bushiness in unidirectional flow (regression, $F_{(1,38)} = 5.5$, $P = 0.02$, $R^2 = 0.13$) and low frequency oscillating flow (regression, $F_{(1,38)} = 6.3$, $P = 0.02$, $R^2 = 0.14$), but not high-frequency oscillating flow (regression, $F_{(1,38)} = 0.41$, $P = 0.52$, $R^2 = 0.01$) (Fig. 3).

Colony feeding effectiveness (feeding/weight) showed similar trends. There was a slight decrease in colony feeding effectiveness with increasing bushiness in uni-directional flow (regression, $F_{(1,35)} = 5.2$, $P = 0.028$, $R^2 = 0.13$) and low-frequency oscillating flow (regression, $F_{(1,36)} = 5.9$, $P = 0.019$, $R^2 = 0.14$), but not in high frequency oscillating flow (regression, $F_{(1,34)} = 3.3$, $P = 0.08$, $R^2 = 0.09$) (Fig. 4). Thus, it can be seen that while bushiness has a weak effect on feeding performance in uni-directional and low-frequency oscillating flow, high-frequency flow seems to mitigate its effect.

Unidirectional flow velocity

There was a significant increase in polyp feeding effectiveness as flow velocity (and consequently particle flux) increased (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 11.42$, $P = 0.003$) (Fig. 5). When the particle concentration was altered to provide equivalent particle flux at all three velocities, there was no difference between any of the flow velocities (Kruskal-Wallis 1-Way ANOVA, $\chi^2 = 1.74$, $P = 0.42$). This suggests that the increase in polyp feeding effectiveness with increasing flow velocity was due to differences in particle availability (flux), not to differences in flow velocity *per se*.

Colony feeding effectiveness (# polyps fed/colony weight) showed a similar trend, with significant differences at equivalent particle concentration (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 8.16$, $P = 0.017$) and no significant differences at equivalent particle flux (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 1.67$, $P = 0.43$) (Fig. 5). Thus differences in colony feeding effectiveness are also due to differences in particle availability, not to differences in flow velocity.

Location within the colony

Polyp feeding effectiveness was not affected by the location (height) of the polyp within the colony. There was

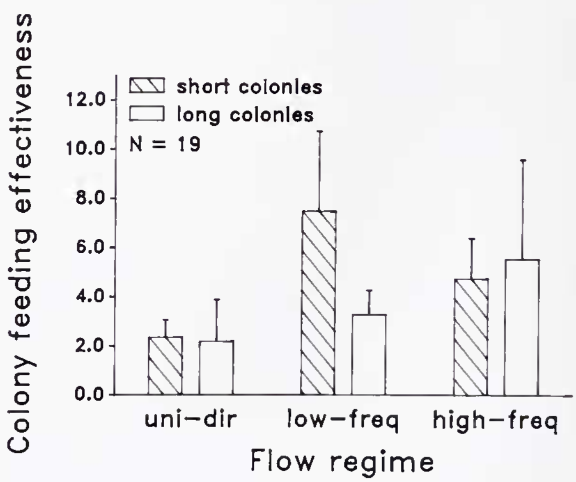

Figure 2. Colony feeding effectiveness (number of fed polyps/colony mass) in uni-directional flow, low frequency (0.33 hz) oscillating flow, and high frequency (1.04 hz) oscillating flow for long (0.083 m) and short (0.033 m) colonies. Error bars are 95% confidence intervals.

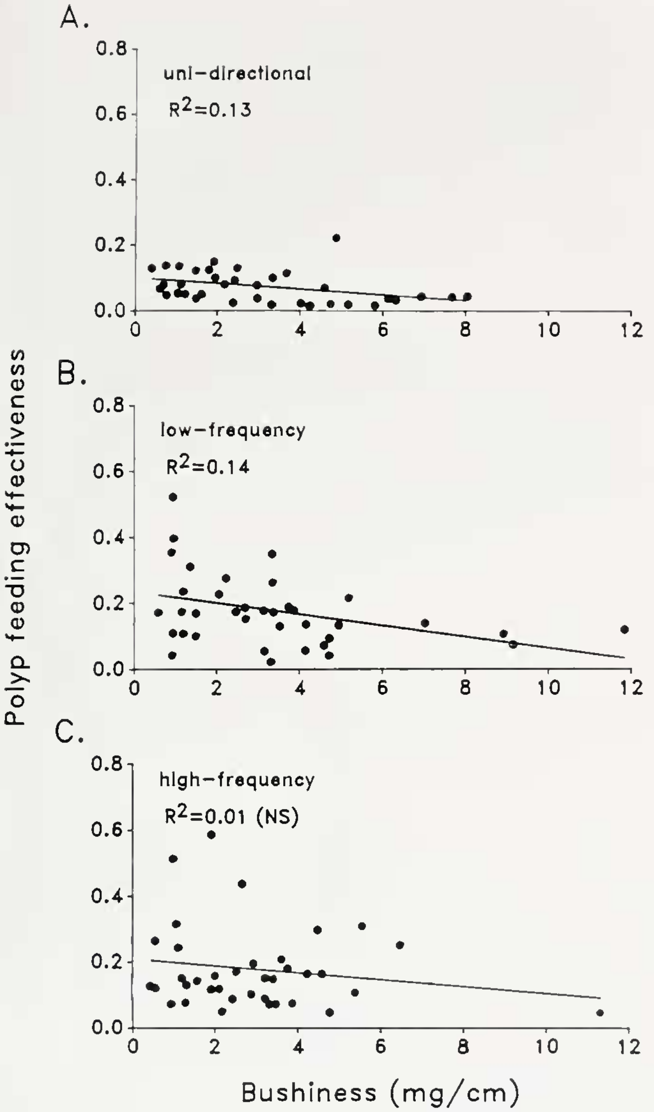

Figure 3. Polyp feeding effectiveness (number of fed polyps/number of polyps capable of feeding) plotted as a function of colony bushiness (colony weight/colony length) for uni-directional flow, low frequency oscillating flow (0.33 hz), and high frequency oscillating flow (1.04 hz).

no significant difference in polyp feeding effectiveness (# polyps fed/# capable of feeding) in polyps from the top or the bottom of the colony (Fig. 6) in any flow regime (nested ANOVA, $F_{(2,228)} = 0.16$, $P = 0.85$).

Discussion

Flow regime and feeding

Four factors strongly affect feeding by flexible organisms in oscillating flow regimes: (1) colony reorientation, (2) fluid resampling, (3) local particle depletion, and (4) reduced relative flow velocity. These factors interact in a complex fashion, making it difficult to predict *a priori* how flow regime will affect feeding. I will briefly discuss each of these effects.

Reorientation

In contrast to rigid organisms, flexible organisms are passively reoriented to changes in flow direction. In uni-directional flow, as the flow velocity increases, the organism tends to be pushed over towards the substratum. The faster the flow, the more the organism leans over. This positions more of the organism within the boundary layer (region of reduced flow velocity adjacent to the substratum), so the flow velocity, and consequently the particle flux, is reduced.

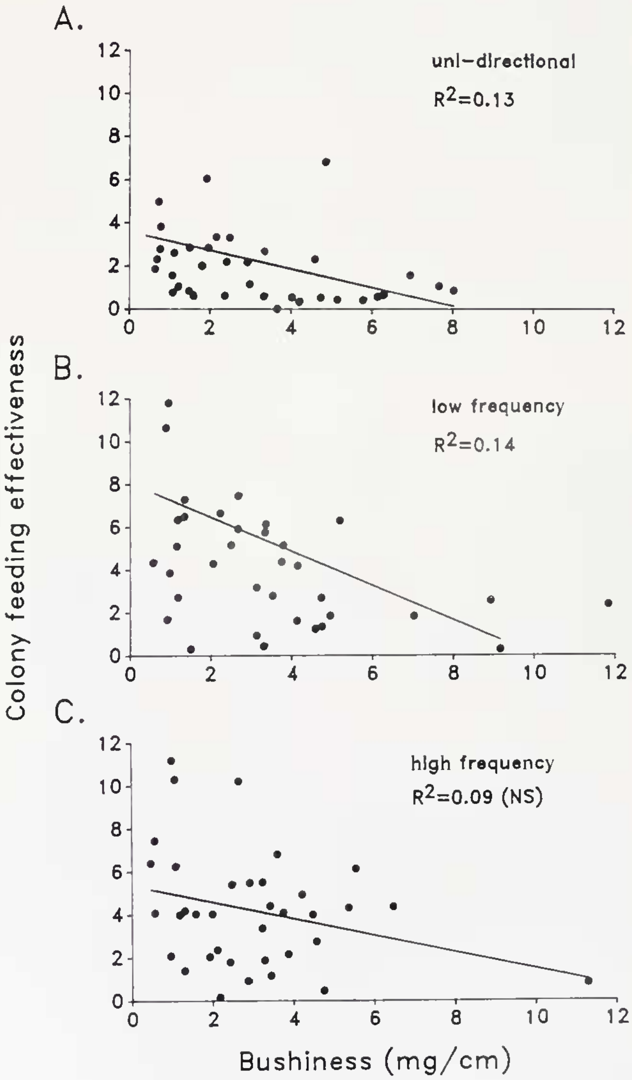

Figure 4. Colony feeding effectiveness (number of fed polyps/colony mass) as a function of colony bushiness (colony weight/colony length) for uni-directional flow, low frequency oscillating flow (0.33 hz), and high frequency oscillating flow (1.04 hz).

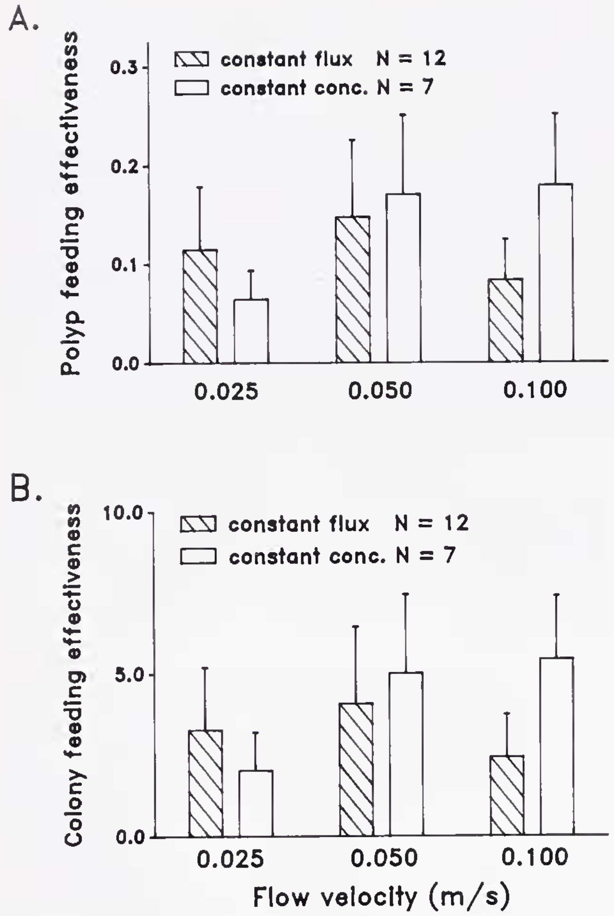

Figure 5. (A) Polyp feeding effectiveness (number of fed polyps/number of polyps capable of feeding) as a function of flow velocity in "slow" (0.025 m/s), "medium" (0.050 m/s), and "fast" (0.100 m/s) uni-directional flow. Data is plotted for experiments done at constant particle concentration (blank bars), in which the particle flux increases with flow velocity, and altered particle concentration (striped bars), where the particle flux is equivalent at all three flow velocities. All error bars are 95% confidence intervals. (B) Colony feeding effectiveness (number of fed polyps/colony mass) in the same uni-directional flow treatments.

Reorientation also reduces local flow velocity (and consequently particle flux) by "self shading." As the colony is pushed parallel to the flow direction, polyps downstream near the tip of the colony are "shielded" from the flow by the upstream polyps. The colony branches collapse together, and the water tends to pass around the entire colony rather than between the colony branches. Water velocity through the colony is thus reduced. This effect was clearly observed by injecting fluorescein upstream of the colony and timing the passage of the dye through the colony. Self shielding has been observed to reduce flow through numerous other benthic organisms. For example, Chamberlain and Graus (1975) described retarded flow through various scleractinian corals caused by "self shading." Okamura (1984) has invoked "shading" as a mechanism by which upstream colonies of the bryozoan *Bugula stolonifera* reduced feeding by downstream colonies.

In oscillating flow, these effects are mitigated. As oscillation frequency increases, the flow direction reverses before the colony has a chance to lean over. The colony tends to maintain an orientation normal to the flow direction and "self shading" is reduced. Thus, based simply on the reorientation effects, one would expect to see enhanced feeding in oscillatory flow relative to unidirectional flow. This prediction is supported by the data of this study and is consistent with the observation that the hydroid *Aglaophenia pluma* grows more rapidly in oscillating than in uni-directional flow (Svoboda, 1970). This enhanced growth may be mediated by higher particle (food) capture rates in oscillating flow.

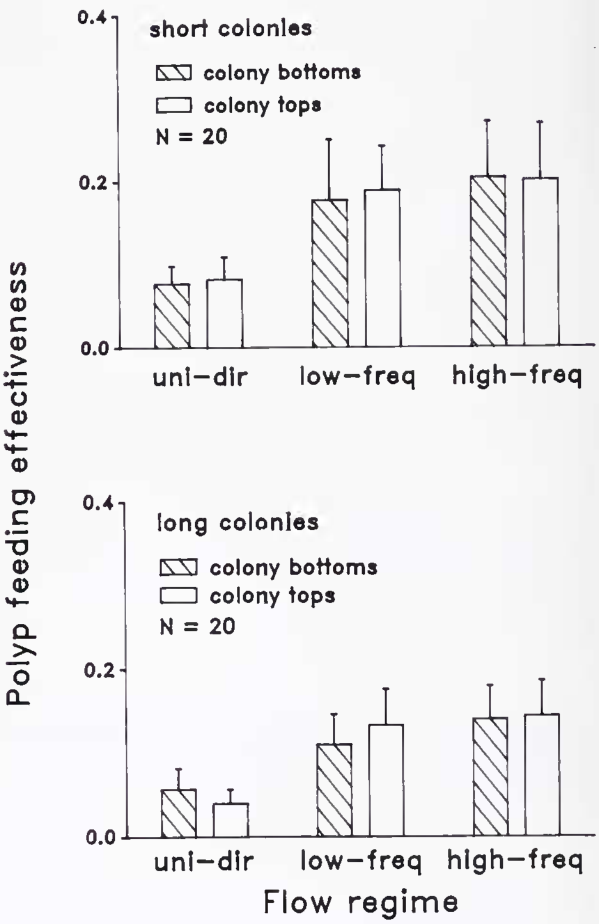

Figure 6. Polyp feeding effectiveness (number of fed polyps/number of polyps capable of feeding) in uni-directional flow, low frequency (0.33 hz) oscillating flow, and high frequency (1.04 hz) oscillating flow. Polyps from the top 25% (blank bars) and the bottom 25% (striped bars) of long (0.083 m) and short (0.033 m) colonies. Error bars are 95% confidence intervals.

Fluid resampling

In oscillating flow, the same "parcel" of water tends to move back and forth repetitively over the colony. The colony thus samples the same volume of water over and over again. The size of this "parcel," and thus the volume resampled, is determined by the amplitude of the oscillation. The amount of new water seen by the colony is a function of the rate of mixing of this parcel with fluid farther away from the colony and the rate of advection (*e.g.*, flow due to the tidal current onto which the waves are superimposed) of water past the colony. Dye blobs injected around colonies in the field show rather long residence times (1–2 min). Similar effects have been seen in the field around gorgonian sea fans in wave surge (Koehl, pers. com.). This is in dramatic contrast to uni-directional flow where water often remains only briefly around a colony before being swept downstream.

As the food particles within the resampled volume of fluid are consumed feeding effectiveness may decrease. Thus, by increasing local particle depletion, fluid resampling in oscillating flow may tend to reduce feeding effectiveness and thus acts to reduce the feeding "enhancement" effect of reorientation.

Local particle depletion

Local particle depletion may occur in oscillating flow as a consequence of fluid resampling. However, local depletion may occur in uni-directional flow even though there is no fluid resampling. In uni-directional flow, passive reorientation (leaning over) of the colony, has the effect of placing the low (basal) polyps in the colony upstream of the more distal polyps. Thus basal polyps may reduce the particle concentration of the water by the time it reaches the distal polyps. Similarly, increasing colony bushiness (or the presence of colonies upstream) may result in local particle depletion, much as the presence of colonies of the ectoproct *Bugula stolonifera* decreased feeding by downstream colonies possibly through local particle depletion (Okamura, 1984). Thus local depletion due to colony reorientation or increasing colony bushiness may reduce feeding effectiveness in uni-directional flow, while local depletion due to fluid resampling may reduce feeding effectiveness in oscillating flow.

The effect of local particle depletion on feeding effectiveness must depend on the rate of transport of particles into the depleted volume of fluid. In oscillating flow, the colony waves back and forth in an undulatory fashion. This caused the branches to "flail like oars" and appeared to increase mixing in the vicinity of the colony. Patterson (1984) has shown that increasing turbulence (in a uni-directional flume) results in more uniform distribution of particle capture throughout colonies of *Alcyonium siderium*, indicating that local mixing can be important to suspension feeders.

Dye blobs injected around the hydroids showed rapid mixing in the wave tank, but were quickly swept downstream away from the colonies in the uni-directional flume. Dye injected around hydroids in the field is rapidly mixed around the colonies, but *Obelia* in the field forms rather dense canopies and the dye is retained within the canopy. The data showing enhanced feeding in oscillating flow relative to uni-directional flow are consistent with the hypothesis that increased local mixing mitigates the effects of local particle depletion.

Reduced relative flow velocity

A reduction in flow velocity relative to the organism is a feature peculiar to flexible organisms in oscillating flow regimes. When the direction of flow reverses, there is a period of time during which the distal portion of the organism is moving *with the flow* as the colony reorients. During this reorientation, the flow velocity (and consequently, the particle flux) relative to the colony tip should be reduced or zero. When the colony has fully reoriented (*e.g.*, when it is completely "strung out" in the direction of flow) the distal region will again experience flow. Longer colonies require a larger amplitude of oscillation to be fully reoriented. For any given oscillation frequency and amplitude, there is a colony length at which a colony never achieves full reorientation before the oscillation reverses.

In light of the "reduced relative flow velocity" (and consequently reduced particle flux) at colony tips, polyp feeding effectiveness near the tips should be lower than polyp feeding effectiveness near colony bases. Further, this difference should be more pronounced in long as opposed to short colonies because long colonies show a greater reduction in relative velocity at the tip than do short colonies (Hunter, 1988). The data do not support this hypothesis. There is no significant difference in feeding effectiveness between the top 25% and the bottom 25% of the colony (Fig. 6).

It is possible that local mixing due to the "flailing" of the branches of long colonies maintains a high local particle concentration; so the reduced water velocities relative to the colony tips do not significantly reduce particle flux. Alternatively, particle retention may be increased at reduced relative velocity. At lower flow velocity particles are less likely to be swept out of the "polyp's grasp." Many authors (*e.g.*, Wainwright *et al.*, 1976; Okamura, 1984; Harvell and LaBarbera, 1986) suggest that particle capture and retention at "high" flow velocities might be a problem for suspension-feeding organisms. It is suggested that flexibility, by reducing "relative" flow velocities, also reduces variability in flow speed and thus facilitates suspension feeding (Wainwright *et al.*, 1976; Harvell and LaBarbera, 1986). Evaluation of these hypotheses will require actual visualization of particle capture.

Flow velocity and feeding

Feeding effectiveness is higher in oscillating than in uni-directional flow at the same average velocity. Yet, the peak velocity in oscillating flow is higher than in uni-directional flow (0.087 m/s *vs.* 0.025 m/s, respectively) and the difference in feeding may simply be due to this difference in peak velocities. Simply increasing flow velocity (from 0.025 m/s to 0.050 m/s) in uni-directional flow at constant particle concentration increases polyp and colony feeding effectiveness (Fig. 6). This is due to an increase in particle availability (flux past the colony). If particle flux is held constant, this increase in feeding with increasing flow velocity disappears (Fig. 6).

By measuring feeding both at constant flux and at constant particle concentration, it is possible to separate effects due to particle availability from effects due to flow velocity *per se.* Most studies have analyzed the effect of velocity on feeding without separating these two confounding effects (*e.g.,* Leversee, 1976; LaBarbera, 1981; Okamura, 1984).

Colony morphology

Increases in colony bushiness (colony weight/colony length) result in a small but significant decrease in both polyp feeding effectiveness (Fig. 4) and colony feeding effectiveness (Fig. 5). As colony bushiness increases, more gastrozooids (mouths) occupy the same volume. Thus, if the volume is well mixed, feeding effectiveness should increase. However, if the volume is not well mixed, and colony feeding results in a local particle depletion, then feeding effectiveness should decrease because of the lack of particles available for consumption. Increased local mixing, by stirring more particles into this depleted volume of water, would tend to restore the original particle concentration. If the effect of bushiness on feeding effectiveness is mediated through particle depletion, high frequency oscillating flow, by increasing mixing, should eliminate the dependence of feeding effectiveness on bushiness. (Dye blobs around the colony dissipate more rapidly in high frequency flow than in low frequency flow, suggesting that mixing is more rapid in the high frequency flow regime.) The data are consistent with this hypothesis (Figs. 3, 4). Clearly, as the dependence of feeding effectiveness on bushiness shows, the effect of changes in morphology on performance may depend on the flow regime. Increasing colony length also decreased feeding effectiveness (Fig. 2). This might be explained as a consequence of low relative flow velocities (and particle flux) near the tips of long colonies. However, there was no significant difference in polyp feeding effectiveness between colony tops and bottoms (Fig. 6). A strong correlation between length and colony bushiness (Fig. 7) may account for the length effect. Since increased bushiness decreased feeding effectiveness (Figs. 3, 4), and since increased length was associated with increased bushiness, then increased length should be associated with decreased feeding effectiveness. If this is so, one would expect to see the effect of length on feeding to be mitigated in high-frequency oscillating flow since bushiness had no effect on feeding in high frequency flow. This is not the case. Bushiness, however, increased rapidly with increasing length (Fig. 7). Long colonies may be so much more bushy than the short colonies that a local particle depletion occurred even in high-frequency oscillating flow.

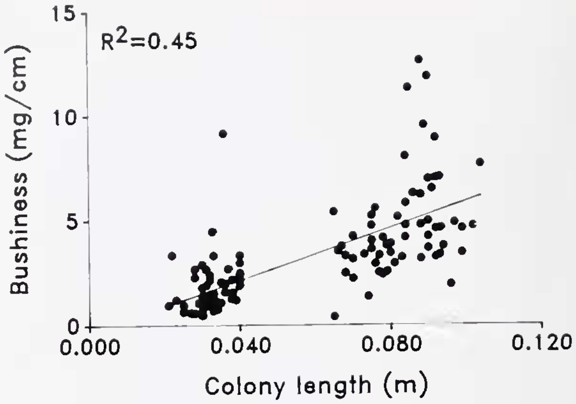

Figure 7. Colony bushiness (colony weight/colony length) as a function of colony length. Bushiness shows a significant increase with increasing colony length (regression, $F_{(1,117)} = 143$, $P < 0.001$, $R^2 = 0.45$).

Flow regime and performance

Clearly an examination of suspension feeding as a function simply of flow velocity may prove misleading if the organism normally lives in an unsteady flow habit. Fluid resampling and reduced relative velocity do not occur in uni-directional flow. The effects of reorientation and local particle depletion may vary greatly with flow regime. In addition, variations in morphology may have different effects on the rate of suspension feeding in different flow regimes. Further, the behavior of the organism may change with changing flow regime. For example, in oscillating flow, the encrusting bryozoan *Membranipora* tends to achieve an attitude with polyps far more distended than in uni-directional flow (pers. obs.). Such changes in behavior or performance with changing flow regime have been documented in many groups (*e.g.,* spionid polychaetes, Taghon *et al.*, 1980; bivalved molluscs, Walne, 1972; bryozoans, Okamura, 1987).

In summary, the flow habitat occupied by flexible organisms is not simply equivalent to the ambient flow regime. Rather, it is a complex interaction of colony morphology and water movement. Factors such as colony reorientation, fluid resampling, local particle depletion, and reduced relative flow velocity may strongly effect the performance of the organism. Further, reduced relative flow velocity and fluid resampling are factors present for flexible organisms in oscillating, but not in uni-directional flow regimes. This fundamental difference between oscillating and uni-directional flow regimes, suggests that it is inappropriate to estimate feeding performance of suspension-feeding organisms in uni-directional flumes if their normal habitat is subject to oscillating flow.

Acknowledgments

I wish to thank my major professor, Dr. M. A. R. Koehl, and Drs. M. H. Wake and J. A. West for providing considerable encouragement and constructive criticism throughout this study. This paper has also profited from a reading by Dr. R. I. Smith. I am grateful to Friday Harbor Laboratories for providing facilities and laboratory space. This work was supported by NSF grants OCE-8201395, OCE-8352459, OCE-851-0834 to Dr. Koehl, and grants to the author from the Lerner Gray Fund for Marine Research, Sigma Xi, and the Zoology Department Graduate Student Research Allocation Committee, University of California, Berkeley.

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